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Natural Sciences

Original article

Diversity and phorophyte preferences of lichens in the Cerro Machín volcano cloud forest (Tolima, Colombia)

Diversidad y preferencias de forófito de los líquenes en el bosque de niebla del volcán Cerro Machín, Tolima, Colombia

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Abstract

Cerro Machín is located in the municipality of Ibagué. It is a volcano with active fumaroles reaching 2650 m of elevation. Montane forest relics mostly cover it, but the forest in the surroundings has been largely replaced by pastureland. We surveyed its lichenized fungi communities focusing on species composition, community structure, diversity, and phorophyte preferences. Thirty-five of the 113 species observed are new reports for the department of Tolima and six of them for Colombia. The overall species richness is the highest reported in the municipality of Ibagué. In the study area, the forest has a good conservation status indicated by the presence of the genus *Sticta*. We registered an average of seven lichenized fungal species per tree, i.e., a low richness, possibly due to the exhausts of the fumaroles. A beta diversity analysis showed a high percentage of rare species. We found evidence of some preference of lichens for bark characteristics, but we did not observe specificity towards tree species.

Keywords: Lichen biota of Colombia; Andean ecosystems; Central mountain range.

Resumen

El volcán Cerro Machín está ubicado en el municipio de Ibagué; alcanza los 2.650 m de altitud y sus fumarolas están activas. En la mayoría de su área se encuentran relictos de bosque montano, en tanto que en sus alrededores éste ha sido reemplazado sobre todo por pastizales. Nuestro estudio evaluó las comunidades de hongos liquenizados, su composición de especies, la estructura de la comunidad, su diversidad y su preferencia de forófito. De las 113 especies observadas, 35 correspondieron a registros nuevos en el departamento de Tolima, de los cuales seis lo eran también para Colombia. La riqueza total registrada es la más alta que hasta ahora se ha reportado en el municipio de Ibagué. En el área de estudio se encontró un bosque conservado y en buen estado, según lo indicó la presencia del género *Sticta*. Un promedio de siete especies de hongos liquenizados se registró en cada árbol, valores de riqueza bajos que pueden deberse a la emisión de gases de las fumarolas. El análisis de la diversidad beta evidenció una proporción alta de especies raras. También se observó que los líquenes presentaban algunas preferencias características de la corteza, pero no de especificidad de especies de árboles.

Palabras clave: biota liquénica de Colombia; ecosistemas andinos, cordillera Central.

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Introduction

The Cerro Machín Volcano (CMV) is one of the most dangerous in Colombia due to its high potential for outbursts, the extent of its deposits, and the magnitude of its eruptions (**Cortés**, 2001). Following the **Holdridge** (1966) classification system, it is situated in the life zones of premontane wet forest (wf-P) and lower montane wet forest (wf-LM) (**Servicio Geológico Colombiano**, 2007). Andean rainforests are seriously threatened by anthropogenic interventions in Colombia, including wood extraction, agriculture, traffic, and urbanization (**Armenteras *et al.***, 2017). Many of these forests have been turned into *Eucalyptus spp*. and *Pinus patula* plantations, with negative effects on the diversity, composition, and structure of lichenized fungi communities (**Ardila *et al.***, 2015; **Simijaca *et al.***, 2018).

Aguirre *et al.* (2008) reported that the Colombian Andean region harbors 1,396 species of lichens representing 89% of all the species in the country according to the checklist by **Sipman *et al.*** (2008). More recently, **Sipman & Aguirre** (2016) reported 1,674 lichen species in Colombia, corrected to 1,672 by **Lücking *et al.*** (2021). The most recent report considerably increased this number to 2,670 species, placing Colombia in the top ten countries with the highest diversity of these organisms (**Moncada *et al.***, 2022). However, the number of species in the Andean region has not been updated.

In Andean ecosystems, lichens are an important biological element associated with tree bark and shrubs. They are pioneers in the colonization of soils and exposed rocks (**Watanabe & Kitagawa**, 2004; **Alfonso**, 2016) and they contribute to the water (**McCune**, 2000) and nutrient cycles, especially the nitrogen input (**Benner *et al.***, 2007). Many studies in Colombia have focused on the Andean ecosystems (**Moncada *et al.***, 2022), documenting an enormous richness in mid and high-mountain zones (**Soto Medina *et al.***, 2021). However, little is known about the lichen biota of volcanic landscapes in the Colombian Andes (**Sipman**, 1989; **Wolf**, 1994) and the factors influencing the colonization by epiphyte communities under these harsh conditions (**Díaz-Escandon *et al.***, 2016). The recent discovery of new species, including *Cora celestinoa*, *Sticta lobarioides*, and *Sticta phyllidiokunthii,* on volcanic mountains in Colombia (**Moncada *et al.***, 2013a; **Lücking *et al.***, 2017), suggest that these ecosystems harbor unique lichen assemblages.

In recent years, research in the department of Tolima has focused on the mid and high altitude mountain forests of the Andean ecosystems leading to the discovery of several new species and new records in diverse groups of organisms (**Neita-Moreno & Ratcliffe**, 2019; **Volkova**, 2020; **Rincon-Gonzalez & Escalante**, 2020; **Rincón-González *et al.***, 2020; **Correa-Carmona *et al.***, 2021; **Fernández-Alonso**, 2021; **Murillo-Serna *et al.***, 2021; **Anganoy-Criollo *et al.***, 2022; **Orejuela *et al.***, 2022; **Sierra-Ariza *et al.***, 2022). These findings show the significance of the department of Tolima as a refuge for the Colombian flora and fauna. However, information about the lichenized fungi in this department is still limited.

Lichen research performed in Tolima includes the report of different species in the premontane plant formation of the upper basin of the Combeima River (**Esquivel & Nieto**, 2003). Additionally, the diversity and composition of lichens in different urban areas of Ibagué (**Barreto & Esquivel**, 2020), lichens as pollution bioindicators in its city reserves (**Díaz-Villanueva & Morales-Nieto**, 2019), and the metabolites of some species of the genus *Sticta* have been evaluated (**Albornoz *et al.***, 2022). One of these studies in Ibagué examined the preferences of lichens towards certain phorophytes (**Zárate-Arias *et al.***, 2019), a topic rarely studied in Colombia (**Soto *et al.***, 2012; **Ardila-Ríos *et al.***, 2015; **Gutiérrez *et al.***, 2019; **Zárate-Arias *et al.***, 2019). Besides phorophyte preferences, the different factors influencing the composition, diversity, and establishment of lichens in tree vertical layers have been the focus of some few studies (**Wolf**, 1993 a b; **Simijaca**, 2011; **Díaz-Escandón *et al.***, 2016; **Simijaca *et al.***, 2018).

Focusing on phorophyte preferences, **Ardíla-Ríos *et al.*** (2015) reported that planting exotic *Eucalyptus* species decreased species richness, possibly influenced by the peeling of the bark. Lichen communities are also sensitive to variations in bark pH (**Wolf**, 1993 a;

Cáceres *et al.*, 2007; **Díaz-Escandón *et al.***, 2016; **Zárate-Arias *et al.***, 2019). **Simijaca *et al.*** (2018) noted that bark roughness affects species composition since certain lichens prefer smooth bark while others tend to grow on rough bark. It is also known that trees with a high number of grooves or lumps on the trunk bark limit the growth of crustose lichens (**Rosabal *et al.***, 2013) and that the age of the trees influences species composition (**Ellis & Coppins**, 2006, 2007). Besides phorophyte features, lichen community composition is influenced by light intensity variations (**Soto-Medina *et al.***, 2012), including forest types or tree layers (**Lücking**, 1999; **Koch *et al.***, 2013; **Käffer *et al.***, 2021; **Koch *et al.***, 2022).

Given the unique characteristics of Cerro Machín: being one of the lowest altitude volcanoes of Colombia, having a strong topography, and the influence of fumaroles, and considering the lack of information about its lichen biota, this region is an exceptional study area to assess the diversity, composition, structure, and phorophyte preferences of its lichen biota.

Materials and methods

Study area

The study area was located 17 km west of the municipality of Ibagué (4°29’11”N and 75°22’54”W), on the eastern flank of the Cordillera Central of Colombia (**Moreno**, 2012). It is part of the San Diego-Machín volcano-tectonic province (**Martínez *et al.***, 2014) (**Figure 1**). The volcanic complex has an area of 13 km^2 and its crater has a diameter of 2.4 km (**Piedrahita *et al.***, 2018) enclosed by three domes with a height ranging between 1,524 and 2,750 m (**Moreno**, 2012). Climatic conditions vary from temperate to warm, with dry and rainy periods throughout the year, a temperature oscillating between 20°C and 22°C, average annual rainfall reaching 1150 mm, and relative humidity of 85% (**Servicio Geológico Colombiano**, 2007).

Sampling

Sampling was done between August 20, 2021, and January 10, 2022, in six field trips. Plots were selected along an altitudinal gradient from the base of the volcano at 2000 m to the top at 2750 m on the southeast and northwestern faces of the main dome. Forests

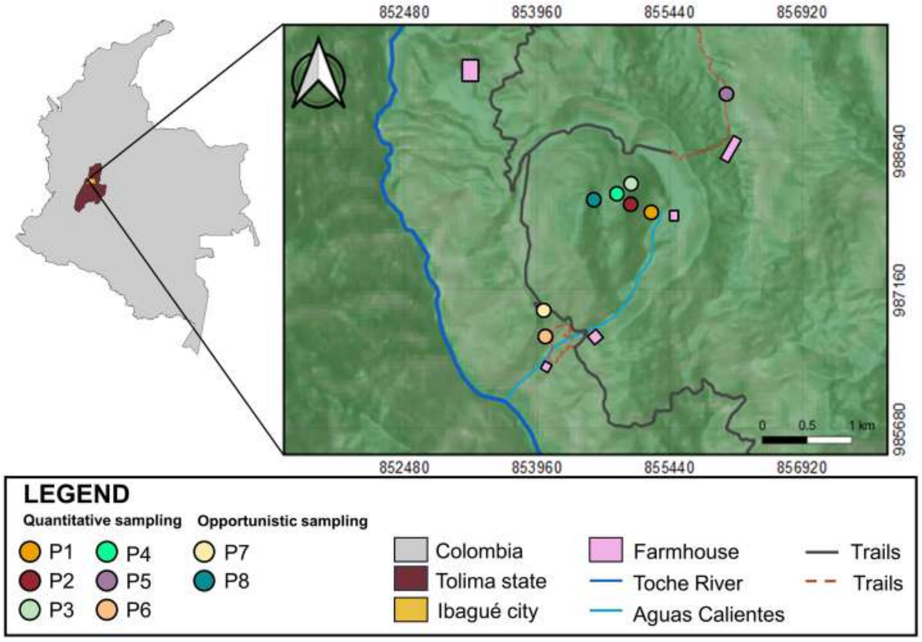

Figure 1. Map of the CMV area with sampling plots georeferencing

were predominant (63%), with some grasslands from local agricultural farms (36%), and streams accounting for 1% of the area (**CORTOLIMA & Universidad del Tolima**, 2008; **Vargas *et al.***, 2007). Plots P1, P2, P3, P4, and P8 were located within the lower montane wet forest (wf-LM) and plots P5, P6, and P7 were in the premontane wet forest (wf-P) (**Holdridge**, 1966). Most of the trees at plot locations ranged from 10 to 25 meters in height and bryophytes predominated in their bark (**Candela & Fernández**, 2021). Other specific characteristics of the zones are detailed in **table S1,** https://www.raccefyn.co/index.php/raccefyn/article/view/2638/4465.

We conducted two types of sampling: first, quantitative, for the analysis of community composition and structure in six plots, P1 to P6 (20 m x 50 m in size) (**Figure 1**, **table S1,** https://www.raccefyn.co/index.php/raccefyn/article/view/2638/4465). We selected four phorophytes from *Weinmannia pubescens*, *Hedyosmum bonplandianum*, *Clusia multiflora*, and *Myrcia popayanensis* species in each of the six plots, adding up to 24 studied trees. For lichen recording, we used 20 cm x 50 cm rectangles fixed to each phorophyte at breast height on the side of the trunk with the highest lichen coverage (**Soto Medina *et al.***, 2012). For the opportunistic sampling, lichens were collected outside the plots on different selected substrates to complement the recorded species (**Sipman**, 1996). Access to P7 and P8 was difficult and the trees suggested for quantitative sampling were never found, so these plots were used for opportunistic sampling (**Figure 1**).

Taxonomy

We identified lichen samples using taxonomic keys, with the help of a dissecting microscope and an OMAX M82ES-SC100-LP100 compound microscope. For genus-level identifications, we used the neotropical lichen key by **Sipman** (2005) and the identification guide of Colombian lichens by **Moncada & Lücking** (preprint). For species-level identifications, we used specialized literature depending on the group (**Rivas-Plata *et al.***, 2008; **Lücking *et al.***, 2009; **Moncada**, 2012; **Moncada *et al.***, 2013b; **Aptroot & Lücking**, 2016; **Gumboski *et al.***, 2018; **Sarlej *et al.***, 2018; **Kitaura *et al.***, 2018; **Kitaura *et al.***, 2019). Chemical tests followed the standardized methods for lichen chemotaxonomy (**Orange *et al.*,** 2001; **McCune *et al.***, 2002) employing potassium hydroxide (K), sodium hypochlorite (C), paraphenylenediamine (P), and iodine (I). The collections are deposited in the herbarium of the University of Tolima (TOLI), with selected duplicates in the Emilio Mahecha Forest herbarium (UBDC).

Phorophyte characteristics

We assessed four parameters for each phorophyte sample. We calculated the diameter at breast height (DBH) of the tree by measuring the circumference at 1.30 m and dividing this value by Pi. We assessed bark pH by collecting superficial bark fragments and analyzing them in the lab. A gram of bark was mixed with 10 ml of distilled water and after an hour, the pH was measured with a digital pH meter (Tester CHECKER® HI 98103) (**Kricke**, 2002). Light intensity was estimated using hemispherical photographs of the canopy above each phorophyte taken with a 180° fisheye lens (OPTEKA Hd2 0.20) mounted on a CANON T3 digital camera. The camera was positioned one meter above the ground and oriented towards the selected side of the tree, with the lens pointing to the magnetic north, determined using a compass (**Koch *et al.***, 2012; **Menezes**, 2013) to standardize the photographs across all phorophytes. The images were analyzed using the Gap Light Analyzer (GLA) software with a setting according to the orientation parameters and the coordinates of each phorophyte (**Frazer *et al.***, 2000). Finally, bark roughness was measured using a twine to draw the bark topography (ridges and hollows) over 10 cm marked with a plastic ruler. The roughness coefficient resulted from the difference between the twine length divided by the 10 cm ruler, a method modified from **Rosabal *et al.***, (2012).

Data analysis

We measured alpha diversity on each of the 24 phorophyte samples as the number of species and using a quantitative diversity measure through the effective number of species of order q0 (richness of species), q1 (number of common or frequent effective species), and q2 (number of dominant effective species) (**Hill**, 1973; **McCune *et al.***, 2002). We evaluated sample coverage to determine the representativeness of the samples relative to the proportion of species found (**Chao & Jost**, 2012) and calculated rarefaction curves to allow comparisons of the richness between the plots studied without considering the frequency of each species (**Gotelli & Colwell**, 2001). For these analyses, we used the Rstudio iNEXT package (**Hsieh *et al.***, 2016; **Moreno**, 2019). We also produced a species accumulation curve to evaluate the completeness of the sampling using the Jackknife 1 estimator and we made comparisons with the rarefaction curves using PAST® version 4.10 (**Hammer *et al.***, 2001).

Beta diversity was measured using Sørensen's relative dissimilarity index calculated for each pair of the 24 phorophyte samples resulting in 276 pairwise comparisons (**McCune *et al.***, 2002). We also employed this index to evaluate the differences between the six plots pooling the four trees within each sampling site.

We evaluated potential phorophyte preferences using non-metric multidimensional scaling (NMDS) with the Sørensen index. The NMDS was conducted with 999 randomizations using a stability criterion of 0.000001 and 100 iterations. Additionally, a two-way cluster analysis was done based on the same Sørensen distance matrix index (**McCune *et al.***, 2002). These two analyses were complemented by an analysis of indicator species with Monte Carlo simulations to test which lichen species had statistically significant preferences for the different groups of phorophytes based on the criteria of significance ($p<0.05$) and marginal significance ($p<0.1$) (**McCune *et al.***, 2002). For the statistical analysis, we used the PC-ORD® software version 5.0 (**McCune *et al.***, 2002).

Results

Taxonomic composition

The inventory of the Cerro Machín volcano resulted in 113 species belonging to 47 genera and 26 families. The quantitative sampling yielded 77 species, 37 genera, and 19 families, and the opportunistic sampling 57 species, 27 genera, and 16 families (**Table 1**). The quantitative and opportunistic sampling shared only 21 species (19%); the quantitative sampling resulted in 55 species (almost 49%) and the opportunistic sampling resulted in 36 species (32%); i.e., the first sampling method yielded a higher richness. *Sticta* was the richest genus, with 11 species, followed by *Parmotrema* (9), *Pyrenula* (7), *Leptogium* (7), and *Cladonia* (7).

Cyanobacterial photobionts occurred in 25 species (22% of those recorded), including the genera *Coccocarpia*, *Cora, Leptogium, Peltigera,* and several species of *Sticta*. Species with chlorococcoid photobiont (green algae) represented 53% of the total, including the genera *Lobariella* and *Yoshimuriella*, and another set of *Sticta* species. Graphidaceae, Pyrenulaceae, and Trypetheliaceae species (amounting to 25% of the species) featured a trentepohlioid photobiont (**Table 1**).

Thirty five (35) species were new records for the department of Tolima: *Allographa macella*, *Aspidothelium cinerascens*, *Cladonia macilentoides*, *Emmanuelia tenuis*, *Hypotrachyna horrescens*, *Kalbographa cabbalistica*, *Leptogium javanicum*, *Lobariella pallida*, *Parmotrema sancti-angelii*, *Phaeographis scalpturata*, *Pyrenula acutispora*, *P. quassiicola*, *Sticta pseudolobaria*, and *Yoshimuriella peltigera.* Additionally, *Allographa superans*, *Architrypethelium penuriixanthum*, *Graphis breussii*, *Lepra tropica*, *Phaeographis coriaria*, and *Pyrenula montocensis* were new records for Colombia (**Figure 2**).

Table 1. Lichenized fungi species at the CMV. Sampling type (P: plots - quantitative sampling; O: opportunistic) and photobiont type (trente = trentepohlioide, cloroc = clorococcoide, cyano = cyanobacteria).

Species	Sampling type	Photobiont
Allographa macella (Kremp.) R. Lücking & K. Kalb*	P	trente
Architrypethelium penuriixanthum Flakus & Aptroot **	P	trente
Arthonia sp.	P	trente
Aspidothelium cinerascens Vain. *	P	trente
Bacidia sp.	P	cloroc
Brigantiaea leucoxantha (Spreng.) R.Sant. & Hafellner	O	cloroc
Chrysothrix chlorina (Ach.) J.R.Laundon	O	cloroc
Cladonia arbuscula (Wallr.) Flot.	O	cloroc
Cladonia didyma (Fée) Vain.	O	cloroc
Cladonia grayi G. Merr. Ex Sandst	O	cloroc
Cladonia macilentoides Ahti & Fleig *	O	cloroc
Cladonia rangiferina (L.) Weber	O	cloroc
Cladonia sp1.	O	cloroc
Cladonia sp2.	O	cloroc
Coccocarpia erythroxyli (Spreng.) Swinscow & Krog	O	cyano
Coccocarpia palmicola (Spreng.) Arv. & D.J. Galloway	O	cyano
Coccocarpia pellita (Ach.) Müll. Arg.	P	cyano
Coenogonium linkii Ehrenb.	P, O	trente
Coenogonium roumeguerianum (Müll. Arg.) Kalb*	P	trente
Coenogonium sp.	P	trente
Coniarthonia sp.	P	trente
Cora applanata B. Moncada, Soto-Medina & Lücking	O	cyano
Cora aspera Wilk, Lücking & E. Morales*	O	cyano
Cora sp2.	O	cyano
Crocodia aurata (Ach.) Link	O	cyano
Cryptothecia sp.	P	trente
Emmanuelia tenuis (Vain.) Lücking, B. Moncada & Gumboski *	P	cloroc
Graphis breussii G. Neuwirth & Lücking*	P	trente
Graphis nanodes Vain.	O	trente
Graphis sp1.	P	trente
Graphis sp2.	P	trente
Graphis superans Müll. Arg. *	P	trente
Herpothallon roseocinctum (Fr.) Aptroot, Lücking & G. Thor	P, O	trente
Heterodermia comosa (Eschw.) Follmann & Redón	O	cloroc
Hypotrachyna horrescens (Taylor) Krog & Swinscow *	P	cloroc
Hypotrachyna imbricatula (Zahlbr.) Hale	P	cloroc
Hypotrachyna laevigata (Sm.) Hale	P	cloroc
Hypotrachyna rockii (Zahlbr.) Hale	P	cloroc
Kalbographa cabbalistica (Nyl.) Lücking*	P	trente
Lecanora sp.	P	trente
Lepra sp.	P, O	cloroc
Lepra tropica (Vain.) Lendemer & R.C. Harris*	P	cloroc
Leptogium andinum P.M. Jørg.	P	cyano

Species	**Sampling type**	**Photobiont**
Leptogium azureum (Sw.) Mont.	P, O	cyano
*Leptogium cyanescens (*Ach.) Körb.	O	cyano
Leptogium foveolatum Nyl.	P, O	cyano
Leptogium javanicum Mont.*	O	cyano
Leptogium phyllocarpum (Pers.) Mont.	O	cyano
Leptogium punctulatum Nyl.	P, O	cyano
Leucodermia circinalis (Zahlbr.) Kalb	O	cloroc
Leucodermia leucomelos (L.) Kalb	P, O	cloroc
Lobariella flavomedullosa B. Moncada, Betanc. & Lücking	P	cloroc
Lobariella pallida (Hook.) B. Moncada & Lücking*	O	cloroc
Lobariella parmeloides B. Moncada & Lücking*	O	cloroc
Lopezaria versicolor (Flot.) Kalb & Hafellner	P, O	cloroc
Malmidea nigromarginata (Malme) Lücking & Breuss	P	cloroc
*Megalospora tuberculosa (*Fée) Sipman	P	cloroc
Parmotrema cetratum (Ach.) Hale	P	cloroc
Parmotrema commensuratum (Hale) Hale	O	cloroc
Parmotrema dilatatum (Vain.) Hale	P, O	cloroc
Parmotrema gardneri (C.W. Dodge) Sérus.*	P	cloroc
Parmotrema louisianae (Hale) Hale*	P	cloroc
Parmotrema robustum (Degel.) Hale	O	cloroc
Parmotrema sancti-angeli (Lynge) Hale *	O	cloroc
Parmotrema subtinctorium (Zahlbr.) Hale *	P	cloroc
Parmotrema zollingeri (Hepp) Hale*	P	cloroc
Peltigera austroamericana Zahlbr.	O	cyano
Peltigera dolichorhiza (Nyl.) Nyl.	O	cyano
Pertusaria tetrathalamia (Fée) Nyl.	O	cloroc
Phaeographis coriaria (M. Wirth & Hale) M. Cáceres, Aptroot, Parnmen & Lücking *	P	trente
Phaeographis dendritica (Ach.) Müll.	P, O	cloroc
Phaeographis scalpturata (Ach.) Staiger*	P	trente
Phlyctis cf. Brasiliensis Nyl.	P	trente
Phyllopsora furfuracea (Pers.) Zahlbr.	P	cloroc
Phyllopsora janeirensis (Müll. Arg.) Swinscow & Krog*	P	cloroc
Phyllopsora parvifolia (Pers.) Müll. Arg.	P	cloroc
Polyblastidium corallophorum (Taylor) Kalb*	P	cloroc
Polyblastidium japonicum (M. Satô) Kalb*	P, O	cloroc
Pseudocyphellaria sandwicensis (Zahlbr.) B. Moncada & Lücking	P, O	cyano
Punctelia sp.	P	cloroc
Pyrenula acutispora Kalb & Hafellner *	P	trente
Pyrenula complanata (Mont.) Trevis.	P	trente
Pyrenula montocensis Lücking*	P	trente
Pyrenula platystoma (Müll. Arg.) Aptroot	P	trente
Pyrenula quassiicola Fée*	P	trente
Pyrenula sp.	P	trente
Pyrenula thelomorpha Tuck.**	P	trente
Ramalina camptospora Nyl.	P, O	cloroc

Species	Sampling type	Photobiont
Ramalina celastri (Spreng.) A. Massal.	P, O	cloroc
Ramalina pusiola Müll. Arg.	O	cloroc
Ramalina usnea (L.) R. Howe*	O	cloroc
Remototrachyna costaricensis (Nyl.) Divakar, Lumbsch, Ferencová, Prado & A. Crespo	P	cloroc
Stereocaulon ramulosum Raeusch.	O	cloroc
Sticta andina B. Moncada, Lücking & Lumbsch	P, O	cyano
Sticta cometia Ach.	P	cyano
Sticta cordillerana Gyeln.	P, O	cloroc
Sticta dilatata (Nyl.) Vain.	O	cyano
Sticta leucoblepharis Tuck. & Mont.	P, O	cyano
Sticta neopulmonarioides B. Moncada & Coca	P	cloroc
Sticta plumbeociliata B. Moncada, A. Suárez & Lücking	P	cyano
Sticta pseudolobaria B. Moncada & Coca*	P, O	cloroc
Sticta roseocyphellata Bungartz, Moncada & Sipman	P, O	cyano
Sticta subfilicinella B. Moncada, Coca & Lücking*	P	cyano
Sticta tomentosa (Sw.) Ach.	O	cyano
Teloschistes exilis (Michx.) Vain.	O	cloroc
Teloschistes flavicans (Sw.) Norman	O	cloroc
Thalloloma astroideum (Müll. Arg.) Staiger*	P	trente
Usnea columbiana Motyka ex Räsänen	P	cloroc
Usnea rubicunda Stirt.	P, O	cloroc
Varicellaria velata (Turner) I. Schmitt & Lumbsch*	P	cloroc
Yoshimuriella dissecta (Sw.) B. Moncada & Lücking	P, O	cloroc
Yoshimuriella peltigera (Vain.) Lücking & B. Moncada *	P	cloroc
Yoshimuriella subdissecta (Nyl.) B. Moncada & Lücking	P	cloroc

Completeness and rarefaction

The quantitative sampling yielded 77 species. The proportion of completeness based on the Jackknife 1 estimator (116 species) was 66.3% (**Figure 3a**). The rarefaction curves showed significant differences between P4 richness values and the other sampling sites. When the values in the curves were close to the total of sampling units (48), an asymptotic pattern was observed, which remained after the extrapolation (**Figure 3b**), evidencing sample coverage oscillating between 96% (Plot 1) and 99% (Plot 6) (**Table S2,** https://www.raccefyn.co/index.php/raccefyn/article/view/2638/4465).

Alpha diversity

Hedyosmum, *Myrcia*, and *Weinmannia* had the same mean richness value per sample (seven lichen species) and *Clusia* had a lower one (five species). Individually, the richest phorophyte was *Hediosmum* 1, with 10 species, followed by *Weinmannia* 5 (9) and *Myrcia* 5 and *Hedyosmum* 3 (both with 8). *Clusia* 4 had the lowest diversity per sample (only 3 species) (**Table S3,** https://www.raccefyn.co/index.php/raccefyn/article/view/2638/4465).

When we examined effective species values at standardized sample coverage (98%), Plot 1 was the most diverse site (^0D= 27; ^1D= 22; ^2D= 19), followed by Plot 5 (^0D= 22; ^1D= 18; ^2D= 16). In contrast, Plot 4 (^0D= 11; ^1D= 8; ^2D= 6) showed less diversity and significant differences in the ^qD values and the rarefaction (**Figure 3b**, **figure 4**). The ^qD values showed the same pattern when comparisons were based on observed values vs. standardized sample coverage (**Table 2**).

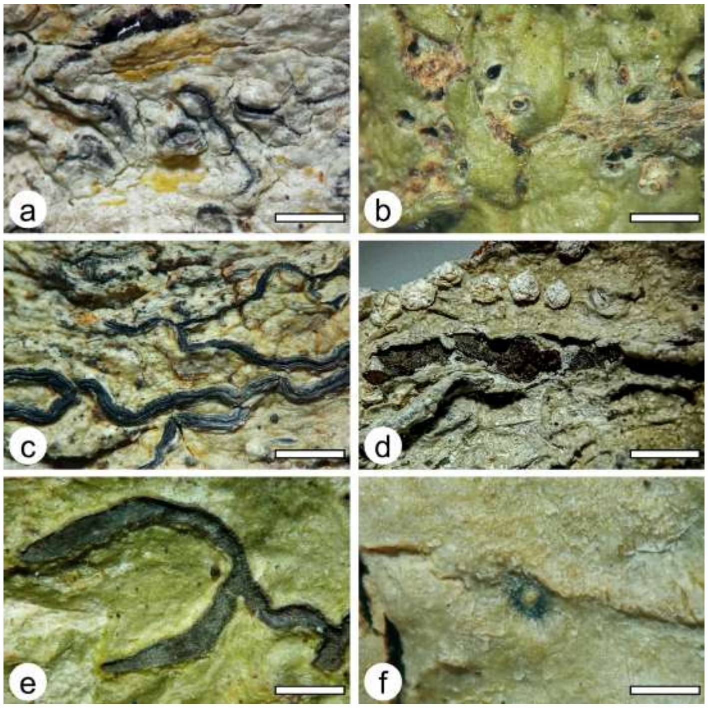

Figure 2. New records of lichenized fungi for Colombia. **a.** *Allographa superans*. **b.** *Architrypethelium penuriixanthum*. **c.** *Graphis* breussii. **d.** *Lepra tropica* (Photo taken to a humid sample making the thallus look greenish). **e.** *Phaeographis coriaria*. **f.** *Pyrenula montocensis*. Scale bar: 1 mm

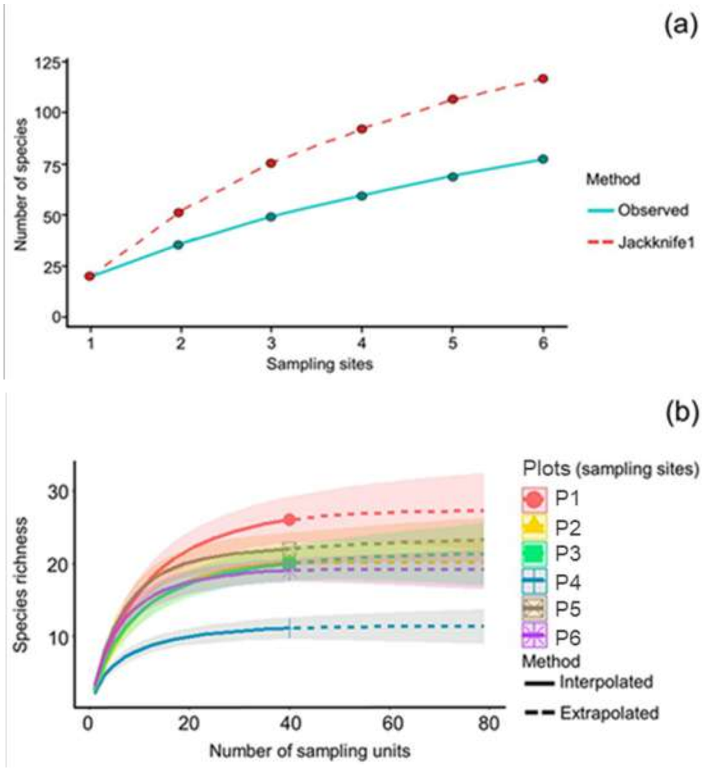

Figure 3. Completeness and rarefaction for the study sites. **a.** Species accumulation curve for the observed species and Jacknife 1 estimator. **b.** Rarefaction curves based on the richness of species

Beta diversity

Beta diversity measured with the Sørensen dissimilarity index showed that 95% of the pairwise comparisons among the phorophyte samples had values greater than 0.7, 4.7% ranged between 0.4 and 0.6, and only 0.3 % had a distance value of 0.1 or lower, indicating high sample heterogeneity (**Figure 5**). Similar patterns were found when comparing the plots, with all pairwise comparisons showing values above 0.68 % (**Table 3**).

The high sample heterogeneity was also evident in the cluster analysis, resulting in distinct groups of phorophytes with few shared species (**Figure 6**). A substantial proportion of the species (57 out of 77, 74%) were rare. Out of these, 41 were very rare, recorded only on one phorophyte, and the remaining 16 were rare, i.e., found on two phorophytes (**Figure 6**).

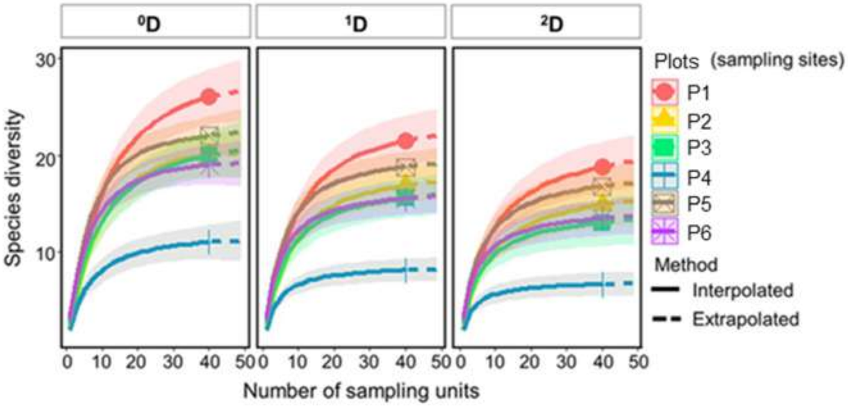

Figure 4. Diversity profiles (^{q}D) for the study sites depicting the effective number of species in each order

Table 2. Values for the three orders of diversity based on the effective number of species for each of the six plots and value comparison based on sample coverage at 98%

Plots	^{0}D	^{1}D	^{2}D	^{0}D [SC 98%]	$^{1}D^{*}$ [SC 98%]	$^{2}D^{*}$ [SC 98%]
P1	26	21.5	18.8	27	22.1	19.4
P2	20	16.9	14.8	20	16.7	14.7
P3	20	15.6	13.1	20	15.8	13.3
P4	11	8.1	6.7	11	8.0	6.6
P5	22	18.8	16.8	22	18.8	16.8
P6	19	15.5	13.5	19	15.3	13.2

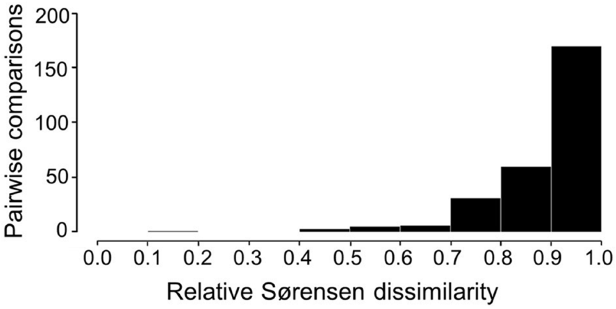

Figure 5. Paired comparisons of beta diversity of phorophytes based on Sørensen dissimilarity

Phorophyte relations

The NMDS analysis (stress = 0.107) did not show a marked separation of lichen communities based on phorophytes, except for *Weinmannia* phorophytes, which formed a separate group in the lower left portion of the diagram (**Figure 7**). Bark pH ($R^{2=}$ 0.21) and richness ($R^{2=}$ 0.25) showed a significant correlation with axis two ($p < 0.1$) (**Table 4**). *Weinmannia* individuals had a lower pH compared to the other phorophyte

Table 3. Paired comparisons of beta diversity among the study sites based on the Sørensen index

	P1	P2	P3	P4	P5	P6
P1	0					
P2	0.78	0				
P3	0.83	0.75	0			
P4	0.95	0.68	0.68	0		
P5	0.83	0.71	0.81	0.82	0	
P6	0.82	0.95	0.9	0.93	0.76	0

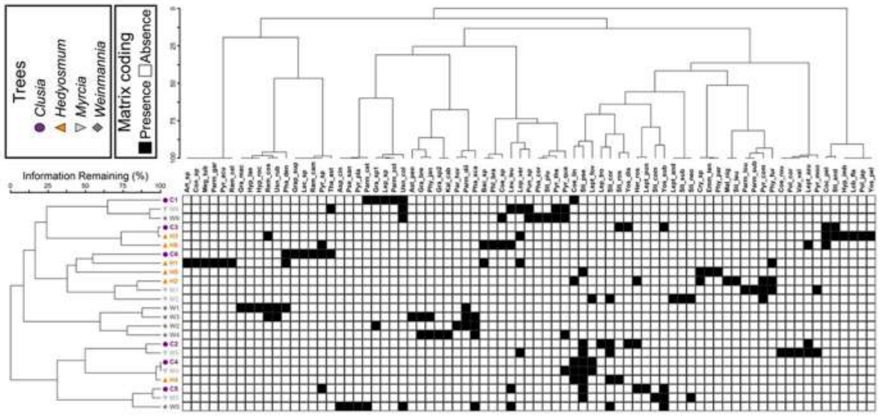

Figure 6. Two-way cluster dendrogram based on the Sørensen similarity index. The numbers (1 to 6) represent the study sites

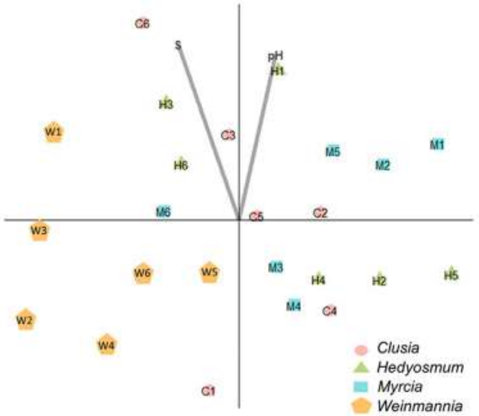

Figure 7. NMDS ordination plot based on the four phorophyte species evaluated showing the correlation of richness and pH parameters with axis two

Table 4. Significance and correlations for the two NMDS dimensions based on the environmental variables.

	NMDS1	NMDS2	r^2	p	
Eleva	0.1774	-0.98414	0.086	0.391	
Roug	-0.98836	0.15213	0.0424	0.626	
DBH	0.2778	0.96064	0.1912	0.098	
Cop	-0.87577	0.48273	0.1169	0.283	
pH	0.23542	0.97189	0.2101	0.087	*
S	-0.35552	0.93467	0.2559	0.056	*

Eleva: Elevation; Roug: Roughness, DBH: diameter at breast height; Cop: Canopy Openness; S: Richness; * significant values

species (**Table S1,** https://www.raccefyn.co/index.php/raccefyn/article/view/2638/4465), although the Kruskal-Wallis test showed no significant differences ($p > 0.05$) among the four phorophyte species for this and other environmental variables (**Table S3,** https://www.raccefyn.co/index.php/raccefyn/article/view/2638/4465).

Clusia included the individuals with the roughest bark (average = 2.25), and *Myrcia* trees had the smoothest bark (1.75). Canopy openness was higher for *Weinmannia* individuals (average = 20.2 W/m^2) and lower for *Hedyosmum* phorophytes (16.8 W/m^2). *Clusia* individuals' trunks had the highest DBH (average = 30.0 cm), and *Weinmannia* individuals had the lowest one (20.2 cm) (**Table S1,** https://www.raccefyn.co/index.php/raccefyn/article/view/2638/4465).

The indicator species analysis (ISA) detected few species with significant preferences for a given phorophyte species, namely *Parmotrema dilatatum* (IV = 50.0) and *Phaeographis scalpturata* (IV=66.7), both significantly related ($p < 0.05$) with *Weinmannia* phorophytes.

Discussion

This is the first assessment of lichenized fungi diversity on the Cerro Machín volcano. The 113 lichen species we found represent 4.2% of the currently documented lichen biota in Colombia. Similar richness values were observed in the area of the Puracé Volcano, where 104 species were collected from 30 phorophytes at three different study sites (**Díaz-Escandón *et al.***, 2016). A study in Parque Los Nevados resulted in 178 species, with 37 to 51 species per study site depending on their elevation (**Wolf**, 1993 a). The Cerro Machín volcano houses a similar number of species; the richness of the altitudinal zones varies between 11 and 26. Exploring undocumented areas offers the opportunity to learn about rare species occupying habitats in need of protection (**Stropp *et al.***, 2020). The number of species recorded in Cerro Machín volcano is remarkable for the department of Tolima, given that previous studies had only documented 21 to 38 species for given localities (**Villanueva & Morales-Nieto**, 2019, **Zárate-Arias *et al.***, 2019, **Barreto & Esquivel**, 2020).

The following species are newly recorded for the Colombian territory (**Figure 2**): *Allographa superans* (Müll. Arg.) Lücking & Kalb, originally described from barks in a tall forest at the Lutindi Forest Reserve, Tanzania (**Müller**, 1894); *Architrypethelium penuriixanthum* Flakus & Aptroot, previously reported in a cloud forest in the Yungas geographical region of Bolivia (**Flakus & Aptroot**, 2016); *Graphis breussii* G. Neuwirth & Lücking, first documented from Venezuela, Amazonas state, near the border with Colombia, on the edges of River Orinoco (**Neuwirth & Lücking**, 2009); *Lepra tropica* (Vain.) Lendemer & R.C. Harris, first discovered in Serra da Chela, Angola, and originally described as *Pertusaria tropica* (**Vainio**, 1901); *Phaeographis coriaria* (M. Wirth & Hale) M. Cáceres, Aptroot, Parnmen & Lücking, originally found in a mossy forest on the island of Dominica in Morne Anglais, at an elevation of 3000 to 3600 m, and then reported as *Phaeographina coriaria* (**Wirth & Hale**, 1978), and, finally, *Pyrenula montocensis* Lücking, first discovered in San Pedro de Montes de Oca in Costa Rica, in an area that is now an urban fabric with factories (**Aptroot *et al.,*** 2008). These new records highlight the importance of tropical cloud forests as a reservoir of biodiversity (**Soto-Medina *et al.***, 2019).

Cloud forests are suitable for colonization by cyanolichens due to their high humidity, mostly acidic bark, and dense canopy cover (**Benítez *et al.***, 2018, **Simijaca *et al.***, 2018, **Chuquimarca *et al.***, 2019). Cyanolichens are an important component in ecosystems for their usual association with specific microhabitats such as preserved primary forests (**Merinero *et al.***, 2014). Accordingly, in the study area, we found several species of cyanolichens, such as *Cora applanata*, *Leptogium foveolatum*, and *Sticta cometia*.

Other lichen biotypes, characteristic of well-preserved forests, were also identified in this study, for example, lichenized fungi with perithectoid and thelotremoid ascomata, considered a good indicator of forest health in the tropics, were abundant (**Rivas-Plata *et al.***, 2008). The presence of lobarioid Peltigeraceae with green algae photobiont is also considered indicative of conserved forests (**Ramírez-Morán *et al.***, 2016). The Cerro Machín volcano yielded nine species of lobarioid Peltigeraceae with green algal photobionts, six species with perithecioid ascomata, and one thelotremoid taxon, indicating that the study area is still relatively well conserved.

Phorophyte preferences have been evaluated based on diverse tree species from various habitats throughout the tropics (**Nöske**, 2004; **Käffer *et al.***, 2009, **Cáceres *et al.***, 2007). In Colombia, stands of *Quercus humboldtii* harbored 41 to 109 species (**Ardila-Rios *et al.***, 2015; **Simijaca**, 2011; **Simijaca *et al.***, 2018) with up to 50 species per tree (**Sipman**, 2006), and studies on *Weinmannia* have recorded 54 to 104 species associated with this genus (**Díaz-Escandón *et al.***, 2016; **Ramírez-Morán *et al.***, 2016). Our study resulted in a total of 29 species on *Weinmannia*, with an average of seven species of lichens per tree, indicating a much lower diversity. However, the lichen richness on *Weinmania* at Cerro Machín volcano is similar to the richness on other phorophytes examined by **Zárate-Arias *et al.*** (2019) in urban green areas in Ibagué (Tolima), with 21 species and an average of three species on each phorophyte. *Clusia* genus has been reported to host between six and eight lichen species per phorophyte (**Soto Medina *et al.***, 2012), while in our study it was between three and six species per tree.

The overall low richness values per tree may be explained by the exhausts from the fumaroles in the study area, which emanate sulfur dioxide as steam at high pressure and temperature. The steam then condenses or dissolves in rainwater that subsequently precipitates as acid rain or fog (**Hochstein & Browne**, 2000). The acid precipitation may affect the lichens directly or indirectly by changing tree bark characteristics such as pH. This effect was observed by **Díaz-Escandón *et al.*** (2016) with sulfur dioxide-containing steam emerging from the El Vinagre River in the area of the Puracé volcano. According to their findings, the trees closest to pollution sources had a lower bark pH, richness, and lichenized fungi coverage, in line with our study, where trees also exhibited low bark pH (between 4 to 6). This was particularly evident in *Weinmmania* phorophytes, which had the lowest pH values of all the studied trees. Also, P4, located 30 m from fumaroles, showed the lowest lichen diversity, and the remaining plots, located 95 to 560 m from them, had increasing diversity. However, P5 and P6 might potentially be affected by anthropogenic intervention in the area given their location near hot springs and trails. There, we observed uncontrolled tourist activities with high traffic resulting in environmental pressures, soil degradation, and vegetation damage. We also observed habitat fragmentation caused by extensive livestock farming in the area surrounding the Cerro Machín volcano, which may contribute to a loss of biodiversity in the region (**CORTOLIMA**, 2020).

Diversity per phorophyte at Cerro Machín volcano was less than in other studies but the contribution of beta diversity to the overall site richness (gamma diversity) coincides with findings in other tropical forests, especially regarding the high number of rare species

(**Cáceres *et al.***, 2007; **Soto-Medina *et al.***, 2012; **Ardila-Ríos *et al.***, 2015; **Díaz-Escandón *et al.***, 2016), which supports the idea that beta diversity is the most important component of lichen diversity in tropical forests (**Komposch & Hafellner**, 2000; **Cáceres *et al.***, 2007). Besides the specific conditions found in tropical forests and their great diversity of microhabitats (**Gradstein *et al.***, 1996; **Victorino**, 2012), sampling techniques may also play a role in the detection of many rare species (**Soto-Medina *et al.***, 2012). In our study, we used the microsquare technique to quantify species frequency, which allowed for the detection of more inconspicuous taxa compared to opportunistic sampling (**Cáceres *et al.***, 2007).

Since rare species add a strong stochastic component to the data, evidence of phorophyte preferences or even the specificity of lichens may be more difficult to detect. In our study, the *Weinmannia* genus was the one that seemed to filter certain lichen species; the subtle trends detected may be explained by the moderate influence of bark pH as seen in the ordination analysis. This is supported by the study of **Cáceres *et al.*** (2007), who also highlighted the influence of bark pH on lichen communities, along with other bark features such as lenticels or shedding. **Díaz-Escandon *et al.*** (2016) also reported that *Weinmannia* trees, with their low average pH (4.15), hosted only three species on average, had less coverage, and even absence of lichens sometimes. Generally, bark acidity directly impacts the lichen thallus, preventing the establishment and reproduction of certain species (**Brodo**, 1973).

Other parameters, such as bark roughness, also influence the composition of lichen communities. Here, we recorded 1.7 to 2.2 averages, relatively high compared to the study by **Rosabal *et al.*** (2013) in Cuba, who reported average values slightly over 1.0 and a negative correlation between species richness and bark roughness. Similarly, **Cáceres *et al.*** (2007) found that the density and size of bark lenticels were negatively correlated with lichen area cover but did not affect the species richness. In another study in Colombia, *Q. humboldtii* trees exhibited a lower bark roughness average and lower richness compared to *Pinus patula* trees (**Simijaca *et al.***, 2018). One may assume that phorophytes with rough barks host a greater number of species, as they allow better thallus adherence. However, particularly crustose lichens may have difficulties establishing and growing on rough bark in competition with three-dimensional macrolichens (**Rosabal *et al.***, 2013).

Light intensity is an important factor in shaping lichen communities. In foliicolous lichens, the community composition was associated mainly with the distribution of light gaps (**Lücking**, 1998; 1999 a, b, c). The degree of canopy openness has also been linked to lichens with specific functional traits (**Benítez *et al.***, 2018; **Soto-Medina *et al.***, 2019). In this sense, **López *et al.*** (2016) identified a positive correlation between richness and luminosity, an effect not detected in the present study, likely because there was no strong variation in canopy openness in our study sites.

On the other hand, certain lichen biotypes have been associated with shady microhabitats in closed-canopy forests. In a sub-Andean forest in Popayán, *Coccocarpia*, *Phyllopsora*, *Sticta*, and *Coniarthonia* lichens were associated with shaded microsites (**López *et al.***, 2016). Also, filamentous lichens belonging to the genus *Coenogonium* are mostly found in shaded forest microhabitats (**Sipman & Harris**, 1989; **Brodo *et al.***, 2001). Certain crustose growth forms represent an adaptation to low light conditions (**Koch *et al.***, 2013), since they may cover large areas with little biomass (**Lakatos *et al.***, 2006; **Koch *et al.***, 2013). Some notable such genera include *Cryptothecia* and *Herpothallon* (**Lakatos *et al.***, 2006; **Benítez *et al.***, 2018); we recorded a high number of species in these genera in Cerro Machín, among them, *Coccocarpia erythroxyli*, *C. palmicola*, *Coenogonium linkii*, *C. roumeguerianum*, *Herpothallon roseocinctum*, *Sticta subfilicinella*, *S. neopulmonarioides*, and *S. tomentosa*. Canopy opening measurements in our study displayed a pattern of homogeneity as to the amount of light entering the understory, with averages ranging from 17% to 20% per phorophyte, considered low in comparison to **Soto *et al.*** (2012), who observed a range from 20% to 40% for this parameter, which influenced the composition of the lichen communities in their study.

In general, our results support other findings on possible lichen preference towards some aspects of tree bark such as pH or structure, but very rarely genuine specificity between lichen and tree species (**Cáceres *et al*.**, 2007; **Soto-Medina *et al*.**, 2012). The absence of phorophyte specificity may be related to the high diversity of trees present in tropical forests since many tree species share traits and there are no obvious differences between them. Phorophyte specificity would be disadvantageous for lichens, as it lowers the abundance of appropriate substrates and involves a lower chance of a lichen species establishment, typically because dispersion of diaspores follows stochastic patterns (**Cáceres *et al*.**, 2007).

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Author contributions

BM and DRM designed the investigation. DRM and HE collected the study material in the field. BM and DRM identified the specimens collected and carried out the work lab. BM, DRM, RL, and DS made the ecological analyses of the information collected, wrote the first manuscript draft, edited the draft, and approved the final version.

Conflicts of interest

The authors declared no conflicts of interest.

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